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Forum

Taxonomic Stability is Ignorance

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Absolute nomenclatural stability is undesirable in phylogenetic classifications because they reflect changing hypotheses of cladistic relationships. De Queiroz and Gauthier's (1990: *Syst. Zool.* 39, 307–322; 1992: *A. Rev. Ecol. Syst.* 23, 449–480; 1994: *Trends Ecol. Evol.* 9, 27–31) alternative to Linnaean nomenclature is concluded to provide stable names for unstable concepts. In terms of communicating either characters shared by species of a named taxon or elements (species) included in a taxon, de Queiroz and Gauthier's system is less stable than the Linnaean system. Linnaean ranks communicate limited information about inclusivity of taxa, but abandonment of ranks results in the loss of such information. As cladistic hypotheses advance, taxa named under de Queiroz and Gauthier's system can change their level of generality radically, from being part of a group to including it, without any indicative change in its spelling. The Linnaean system has been retained by taxonomists because its hierarchic ranks are logically compatible with nested sets of species, monophyletic groups, and characters. Other authors have offered conventions to increase the cladistic information content of Linnaean names or to replace them with names that convey cladistic knowledge in greater detail; de Queiroz and Gauthier sacrifice the meaning of taxon names and categorical ranks in favor of spelling stability.

> It is apparent that a classification that has as its purpose the expression of phylogenetic relationships must change as concepts of relationships are changed (Nelson, 1973: 354).

> There is a strong traditional feeling that stability of some sort is important in classification, especially in regard to nomenclature. But when classifications are presented as biological hypotheses, then we must question the usefulness of stability (Gaffney, 1979: 103).

INTRODUCTION

De Queiroz and Gauthier have argued for a "phylogenetic system of biological nomenclature" (de Queiroz, 1988; de Queiroz and Gauthier, 1990, 1992, 1994) because "the current nomenclatural system's basis in the Linnaean taxonomic categories promotes neither explicitness, universality nor stability with regard to the phylogenetic meanings of taxon names" (de Queiroz and Gauthier, 1994: 28). While we would suggest that stability is undesirable in a system of names whose purpose is to reflect scientific hypotheses, de Queiroz and Gauthier's alternative is in fact less stable than the Linnaean system by any meaningful measure.

NAMES AND INFORMATION

The "meaning" of a taxon name for de Queiroz and Gauthier seems to be nothing more than a group

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including the common ancestor of two specified species and all its descendants. Since every pair of species shares a common ancestor at some level and taxon names in their system are without ranks, any two species may constitute a higher taxon and no information is imparted by names regarding whether one such arbitrary taxon is more or less inclusive than the next. For most cladists, the "meaning" of taxon names is either taken to refer to species or to monophyletic groups of species (i.e. taxa) or the hierarchic distribution of synapomorphies implied by such nested taxa (Hennig, 1966; Farris, 1979; Nelson and Platnick, 1981). Character distributions are the evidence for, and point to logical choices for, higher taxa.

According to de Queiroz and Gauthier (1994: 30, box 5) "Under a phylogenetic system of nomenclature, names retain their associations with particular clades or ancestors despite changes in ideas about relationships". Consider one of their examples, in which Agamidae are defined as "the clade stemming from the most recent common ancestor of the species represented by open [squares]", and Chamaeleonidae as "the clade stemming from the most recent common ancestor of the species represented by filled [squares]" (Fig. 1A). Because of a change in ideas about relationships in the example, Chamaeleonidae become nested within Agamidae (Fig. 1B). Among the putative advantages of their approach are the avoidances of paraphyletic taxa and of splitting and lumping (de Queiroz and Gauthier, 1994: boxes 2, 3).

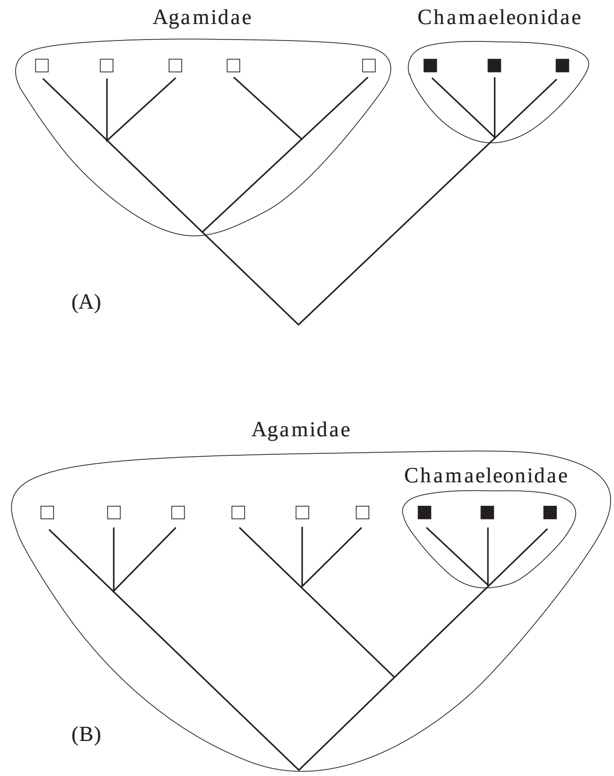

FIG. 1. In the system of nomenclature proposed by de Queiroz and Gauthier names retain their associations with particular clades or ancestors despite changes in hypotheses of relationships. (A) Relationships implied by an earlier classification: see text for definitions of taxa. (B) Revised hypothesis of relationships based on new data or methods of analysis. Modified and redrawn from de Querioz and Gauthier, 1994.

Paraphyletic taxa have long been avoided in the Linnaean system by referring to a cladogram and naming monophyletic taxa (Hennig, 1966). De Querioz and Gauthier claim an advantage in that their taxa cannot be paraphyletic. This is a function not of a superior nomenclatural system but of two-taxon statements that are phylogenetically uninformative (Hennig, 1966). Reference to a cladogram is similarly required to avoid paraphyly in three-taxon statements.

Lumping and splitting are supposedly bad, yet in the Linnaean system they simply reflect changes in phylogenetic hypotheses or choices about which clades one wishes to name formally. For the nomenclatural system proposed by de Queiroz and Gauthier they are bad since they change the contents (meanings) of names that are inflexible. Unfortunately, they are not avoided as claimed. When species are added to, or removed from, a pre-existing name in the de Queiroz and Gauthier system, what has occurred is lumping or splitting with no recourse for indicating changes in relative inclusiveness of a taxon.

In this example, what used to be a family (Chamaeleonidae) becomes part of another family without changing its Latin ending (i.e. spelling), since de Queiroz and Gauthier's nomenclature is rankless. The Linnaean system does not provide precise cladistic information unless used in conjunction with a cladogram. However, the rankless nomenclature is even less informative than the Linnaean system. Consider two beetle families, Dasyceridae and Staphylinidae. If they are hypothesized to be monophyletic and ranked as families, it may be assumed that, as two families, one is not nested within the other. If, as was the case, subsequent phylogenetic analyses suggest that Dasyceridae are a sub-clade of Staphylinidae, the subordinate ranking of the clade as Staphylinidae: Dasycerinae continues to tell us something of its relative relationship to the more inclusive Staphylinidae. However, because in the de Queiroz and Gauthier system one family name can be nested within another, it is no longer certain that one family name excludes other families.

Because de Queiroz and Gauthier's names, by definition, refer to monophyletic taxa, such names are permanent even if subsequent cladistic analyses find that a taxon contains elements that do not fit the original taxon definition and those elements are removed from the group (e.g. Fig. 2, redrawn from de Queiroz and Gauthier, 1990, figure 2). Alternatively, if some elements formerly considered to be outside the taxon are later hypothesized to be included within the taxon, they must be incorporated, changing the contents of the taxon without any corresponding change in terminology. The result is stable names for unstable concepts.

Although obvious, it may be added that categorical ranks play a useful role in the efficient communication of phylogenetic ideas. As Nelson (1973: 349) observed, "For the purpose of producing hierarchical classifications expressing phylogenetic relationships, a convention for subordination may therefore be necessary". Simply put, it is possible to convey relatively precise information about genealogy by stating that one taxon is included in another, more inclusive one (Farris, 1979: 518).

Of the three kinds of definitions proposed by de Queiroz and Gauthier (1990: 310), two (node- and stem-based) are not related to characters. Regarding the third one, the character-based definition, it is said that: "... the character used in an apomorphy-based phylogenetic definition is simply a means of specifying an ancestor. The definition does not imply the presence of the character in all organisms of the taxon, for these characters may be lost in some descendants of the specified ancestor" (de Queiroz and Gauthier, 1990: 310). If so, how can it be known which taxa are included in the group? In Fig. 2 and without referring to a cladogram, how are we to know whether Younginiformes is part of Lepidosauria or not? De Queiroz and Gauthier suggest that the character-based approach cannot be used because characters may or may not be present in all of the members of a taxon.

This phenetic character concept runs counter to the phylogenetic tradition of viewing characters as hypotheses (e.g. Cracraft, 1981; Patterson, 1982). A character is an original attribute and all of its subsequent modifications (Platnick, 1979). It does not need to appear under the same phenetic guise in order to be present in descendant species of a common ancestor. Stated another way, constancy does not mean the absence of variation (Nixon and Wheeler, 1992). Under de Queiroz and Gauthier's strictly phenetic view of characters, the only way of understanding the contents of a taxon is either to know the cladogram that the author used or to enumerate all the included components. Names of taxa related to the evidence from which they are derived obviate the need for such enumeration, making the Linnaean system comparatively more informative than de Queiroz and Gauthier's system, which has little information content at all.

A taxon name is defined by de Queiroz and Gauthier (1990: 310) in one of three possible ways, yet always refers to a hypothetical common ancestor and all of its descendant species. Once such a name is proposed, it remains valid eternally because at some level any two specified taxa will have a common ancestor. As Nelson and Platnick observed, "If life on earth had a common origin, then any two species we might choose will be related by common ancestry at one level or another (A and B have a common ancestor), even if the level is that of all organisms" (1981: 41). In this sense, a taxon with two "types" is potentially more confusing than one with a single type.

Consider one hypothetical example. In a group composed of A, B, C and D, taxon "1" is defined as the clade stemming from the most recent common ancestor of A and B, and "2" as the clade stemming from the most recent common ancestor of C and D. Taxon "3" is the ancestor of B and C (Fig. 3A). Assume that in a later analysis it is found that B is more closely related to C than to A or D (Fig. 3B). Because of the "stability" of the names, "2" will include C-B-D (it is still considered the ancestor of C and D). "1" will include all four groups because it is defined as the ancestor of A and B. Names that at the beginning represented sister groups end up being nested one within the other (e.g. 1 and 2) as in the example in Fig. 1A and B (Chamaeleonidae and Agamidae). Further, due to their system's "stability", taxon "1", which initially included only A and B, becomes more general than "3", which included all four taxa.

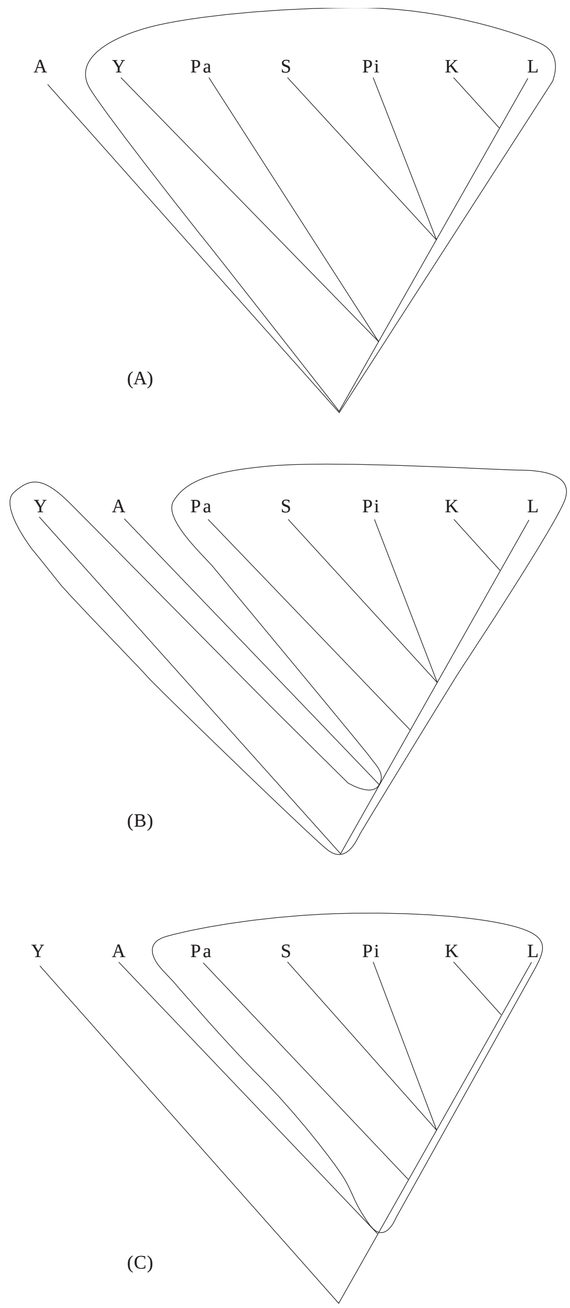

FIG. 2. Hypothetical changes in the relationships of one taxon due to change of ideas about the relationships of one component (Y). (A) Phylogenetic relationships within Sauria, with bubble encircling Lepidosauriomorpha as its name was defined by Gauthier et al. (1988). (B) Hypothetical change in ideas, which seems to imply paraphyly when the content rather than the definition is considered. (C) Actual limits and monophyly of Lepidosauriomorpha under the revised relationships according to the definition as stated. Abbreviations: A, Archosauria; Y, Younginiformes; Pa, Palaeagama; S, Saurosternon; Pi, Paliguana; K, Kuehneosauridae; L, Lepidosauria. Adapted from de Querioz and Gauthier, 1990.

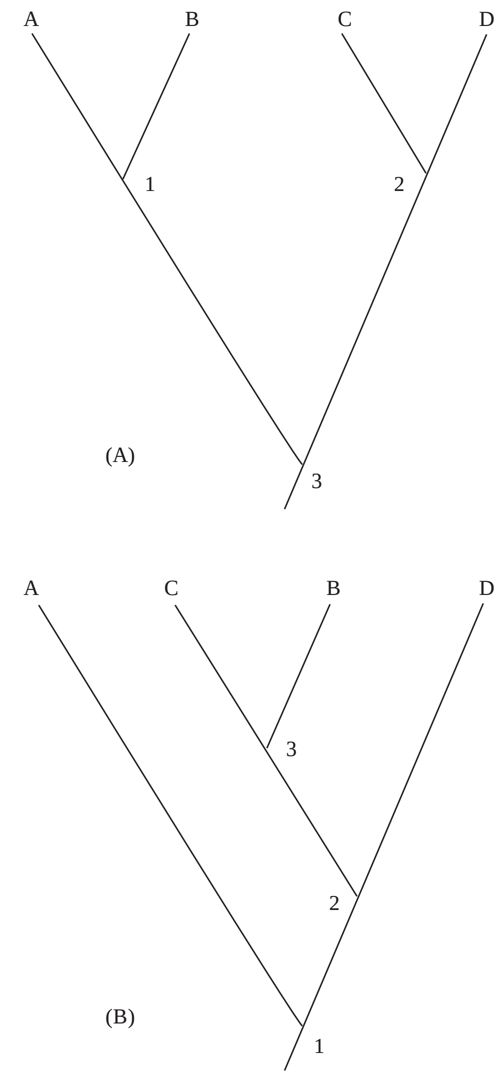

FIG. 3. Hypothetical changes in sister-group relationship without change in "meaning" of names. (A) Original hypothesis. (B) Modified hypothesis (see text for explanation).

The "stability" of a name that points to a taxon for which both position in the cladogram and information content are free to change unpredictably can hardly be considered an advantage.

Our hypothetical examples could be contrived to show an extreme situation, so consider a real example. Laurin and Reisz (1995) recently re-examined the classification of amniotes. Figure 4A and B depicts cladograms from Gauthier et al. (1988: 139) and Laurin and Reisz (1995: 171), redrawn in the same style to facilitate comparison. Based on the re-evaluation of the data on Testudines, Laurin and Reisz proposed this

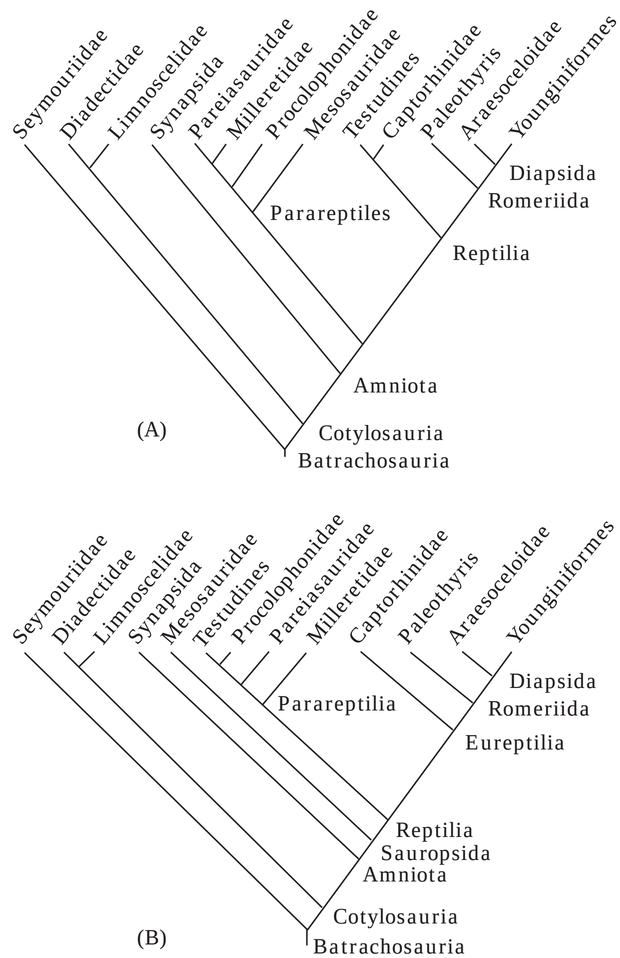

FIG. 4. Changes in content of "Reptilia" under two different hypotheses. (A) Original hypothesis (redrawn with permission from Oxford University Press from Gauthier et al., 1988). (B) New (Laurin and Reisz) hypothesis. Modified and redrawn from Laurin and Reisz, 1995.

new cladogram. The groups basal to Amniota did not change, and neither did Romerida or Diapsida. There were significant changes, however, in the relationships between these two nodes. Anapsida (Testudines+Captorhinidae) were "restricted here to extant turtles, and all other extinct taxa that are more closely related to them than they are to other reptiles" (Gauthier et al., 1988: 142; see Fig. 4A). This group is not present in the second cladogram (Fig. 4B), where Testudines are included in Parareptilia and Captorhinidae in Eureptilia.

Reptilia were "restricted to the most recent common ancestor of extant turtles and saurians (i.e. Younginiformes sensu Laurin and Reisz), and all of its descendants" (Gauthier et al., 1988: 142). In the Gauthier et al. cladogram (Fig. 4A), Reptilia included Testudines+Captorhinidae and ((Younginiformes+Araesoceloidea) Paleothyris). Parareptiles, not a formal name, included Pareiasauridae, Milleretidae, Procolophonidae and Mesosauridae. In the new cladogram, Reptilia include what used to be Reptilia plus parareptiles, except for Mesosauridae which have assumed a position basal to reptiles. The Reptilia remain nominally monophyletic (they must by definition), but their content has changed substantially. Thus its information content is neither stable nor universal, and its informativeness is hopelessly diminished by these two usages of the same taxon name. If changes in our knowledge of turtles can have such a profound influence on a classification of the Amniota, imagine the "stability" in store for lesser-known taxa.

Given de Queiroz and Gauthier's system, a taxon name, once defined as a common ancestor of two taxa and all its descendants, remains valid for use in any conceivable classification that includes these two taxa. Their supposedly "phylogenetic" names are in fact independent of any particular cladogram and can even be proposed without an articulated phylogenetic hypothesis.

DISCUSSION

As Gaffney (1979) observed, in taxonomy stability is ignorance. Taxon names are simply a device to promote unambiguous communication and to provide biologists with a shorthand notation for hypothesized monophyletic groups. Changes in classifications and names are desirable reflections of the growth of phylogenetic knowledge. Categorical ranks are useful as a relative expression of degree of inclusivity of particular taxon names.

In the de Queiroz—Gauthier approach a family name can be subsumed within a genus name, resulting in a complete loss of any hierarchic structure among names.

Limitations of the Linnaean system are well known to cladists. Hennig (1966) insisted upon the need for direct correspondence between cladograms and formal classifications, and concordant ranks for sister taxa. Hennig also experimented with a numerical, sub-ordinated system for more information content in the classifications.

Other authors have taken advantage of the hierarchical structure of both cladograms and Linnaean categorical ranks and sought to modify the system to reflect cladograms better, e.g. Cracraft (1974), Farris (1976), Nelson (1972, 1973), Schuh (1976), Wiley (1979, 1981).

Thoughtful studies of alternatives to the Linnaean system have focused on ways to communicate precisely cladogenetic relationships (e.g. Papavero et al., 1992; Papavero and Llorente-Bousquets, 1993). The ability to redraw a cladogram in detail from a series of formal names is a laudable goal and a potential advance over the Linnaean system.

The de Queiroz—Gauthier recommendations, unfortunately, aim for nominal stability at the expense of cladistic information content and the flexibility necessary to reflect improved cladistic hypotheses and associated applications of names. As Gaffney (1979: 103) observed, "the maintenance of names for discarded concepts seems useless and misleading". This is ultimately why their definition of taxon names through reference to the common ancestor of two taxa is problematic.

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